

Physiological suppression eases in Damaraland mole-rat societies when ecological constraints on dispersal are relaxed

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ABSTRACT

In many vertebrate societies, subordinate females exhibit down-regulated reproductive physiologies relative to those of dominants, a condition commonly termed physiological suppression. Research into the causes of physiological suppression has focused principally on the role of the subordinate's social environment (typically the presence of the dominant female and/or an absence of unrelated males within the group), while few studies have considered the additional role that the physical environment may play. Here we present new evidence from wild Damaraland mole-rats, *Fukomys damarensis*, revealing that physiological suppression among subordinate females eases markedly during the annual rains (a time when ecological constraints on dispersal are relaxed), despite the continued presence of the dominant female and in groups that contain no new immigrant males. Subordinate females showed substantially higher pituitary sensitivities to GnRH challenge during the wet period than the dry, a contrast that cannot be attributed to between-female differences (as it holds for paired within-female comparisons), associated changes in body mass (as our analyses control for this), or concomitant reductions in physiological stress (as their urinary cortisol concentrations were actually higher in the wet period). We suggest that our findings reflect selection for the maintenance of reproductive readiness among subordinate females during high rainfall periods, given the increased likelihood of encountering dispersal and/or mating opportunities with extra-group males when ecological constraints on dispersal are relaxed. These findings reveal new complexity in the processes that regulate physiological suppression, suggesting a key role in some species for changes in the physical as well as social environment.

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Introduction

In many vertebrate societies, subordinate females breed at low rates and show down-regulation at one or more levels of their reproductive endocrine axes relative to those of dominants, a condition commonly termed physiological suppression (Abbott et al., 1997; Bennett et al., 1999; Schoech et al., 2004; Young, 2009). To date, research into the causes of physiological suppression among subordinates has focused principally on the likely importance of two key aspects of their social environment (reviewed in Young, 2009). First, subordinate females commonly exhibit down-regulated reproductive physiologies when in the presence of the dominant female (e.g. Clarke et al., 2001; Saltzman et al., 2009). This may be due either to the subordinate exercising physiological restraint given a threat of interference by the dominant (Young et al., 2008; Saltzman et al., 2009) or to the dominant forcibly down-regulating the subordinates'

fertility by subjecting them to chronic stress (e.g. Young et al., 2006). Second, subordinate females commonly exhibit down-regulated reproductive physiologies when lacking unrelated mates within their groups, a condition that most likely reflects an inbreeding avoidance mechanism (e.g. Cooney and Bennett, 2000; Carlson et al., 2004). Comparatively little work, however, has considered the extent to which subordinate females may also modulate their reproductive physiologies according to changes in their physical environment, which is perhaps surprising as such changes may markedly affect a subordinate's expected fitness payoff from maintaining their fertility.

In many social vertebrates, for example, a subordinate's reproductive potential is limited by ecological constraints on extra-group movement and dispersal, which reduce their chances of encountering extra-group mates or breeding independently (Koenig et al., 1992; Hatchwell and Komdeur, 2000; Young et al., 2007; Young and Monfort, 2009). Wherever variation in the strength of such ecological constraints does affect a subordinate's expected fitness payoff from maintaining their fertility, subordinates may be expected to modulate their reproductive physiology accordingly (favoring up-regulation when constraints are relaxed, to ensure reproductive readiness). Reproductive sensitivity to ecological constraints may therefore be at

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its most apparent in species that experience strong yet variable constraints on dispersal and independent reproduction.

One cooperative vertebrate that experiences acute yet variable constraints on dispersal is the Damaraland mole-rat, *Fukomys damarensis* (formerly known as *Cryptomys damarensis*; Kock et al., 2006). Damaraland mole-rats live in the deserts of southern Africa, where for much of the year the compacted-sand substrate through which they dig their foraging and dispersal tunnels is extremely costly to work (Lovegrove, 1989); an ecological constraint that is thought to have favored the evolution of delayed dispersal (Jarvis and Bennett, 1993; Jarvis et al., 1994; Faulkes et al., 1997). This constraint relaxes markedly, however, during periods of sustained rainfall, which soften the sands and stimulate prolific excavation and dispersal by subordinates of both sexes (to either found new colonies or, among males, to seek matings or immigration opportunities in other groups; Jarvis and Bennett, 1993; Hazell et al., 2000; Burland et al., 2004). A subordinate female's expected fitness payoff from maintaining her fertility is likely to be much higher during such periods, not only because her own chances of successful dispersal are higher, but because her chances of encountering extra-group males with which to mate and/or disperse are also expected to increase (Jarvis and Bennett, 1993; Hazell et al., 2000; Burland et al., 2004). In this study we therefore test the prediction that subordinate female Damaraland mole-rats, who exhibit marked physiological suppression (Bennett et al., 1999), should respond to the relaxation of ecological constraints associated with heavy rainfall by reducing the extent of their reproductive down-regulation.

Damaraland mole-rats live in colonies of 2–40 individuals in which the dominant female monopolizes reproduction and offspring of both sexes delay dispersal and help to rear the dominant's young (Jarvis and Bennett, 1993). The complete suppression of subordinate female reproduction arises through a block on ovulation, which can be attributed to the down-regulation of their pituitary sensitivity to gonadotrophin releasing hormone (GnRH; Bennett et al., 1999; Molteno and Bennett, 2000). The suppression of pituitary sensitivity to GnRH is mediated, at least in part, by two aspects of their social environment: the presence of the dominant female and a lack of unrelated males within the group. On removal from the dominant female, subordinate females show significant increases in pituitary sensitivity to GnRH and begin to ovulate spontaneously (Bennett et al., 1999; Molteno and Bennett, 2000). The introduction of an unrelated male to a subordinate female housed with the dominant female, however, also leads to an increase in the subordinate's pituitary sensitivity to GnRH, as well as copulations with the new male and extreme aggression among the females (Cooney and Bennett, 2000).

While such social factors clearly play a key role in precipitating physiological suppression, there is limited evidence to suggest that subordinate females may also modulate their reproductive physiologies according to changes in their physical environment. A group of subordinate females collected during a wet period had higher pituitary sensitivities to GnRH than another collected during a dry period (Molteno and Bennett, 2002). However, marked differences in body mass between the two groups, coupled with a lack of longitudinal data on their colonies, leave it possible that these physiological differences instead reflect between-female differences in age and/or body condition or a response to recent male immigration.

In this study we use longitudinal data from a wild population of individually identifiable Damaraland mole-rats to investigate: (i) whether subordinate females up-regulate their reproductive physiologies during high rainfall periods (increasing either their baseline LH concentrations or pituitary sensitivity to GnRH); (ii) whether any such changes could be attributable simply to associated changes in body mass or social context; and (iii) whether any reproductive up-regulation detected could be due instead to a concomitant reduction

in the extent of socially-induced stress experienced by subordinates (as evidenced by a reduction in their urinary cortisol concentrations). In addition, we investigate whether the focal high rainfall period does elicit the predicted increase in extra-group movement and dispersal.

Methods

Study population and trapping methods

This study uses data arising from the longitudinal monitoring of Damaraland mole-rat colonies in the semi-arid wilderness of Tswalu Kalahari Reserve (27°22'S, 22°19'E), in the Northern Cape province of South Africa, between 2004 and 2006. The study site lies in a wide basin of thorny Kalahari bushveld, sparsely vegetated with grasses (*Eragrostis*, *Stipagrostis*, *Aristida*, and *Schmidtia* species), bushes (*Acacia mellifera*, *Rhigozum trichotomum*, *Grewia flava* and *Lycium cinereum*) and trees (*Acacia erioloba*, *Acacia haematoxylon* and *Boscia albitrunca*). The average annual rainfall over the period 2001 to 2008 was 297 mm (range 153–459 mm), much of which fell in a limited number of heavy storms unpredictably distributed throughout the hotter summer months (October to April; average maximum daytime temperature = 35.2 °C; average monthly rainfall = 39.6 mm), while comparatively little fell during the winter (May to September; average maximum daytime temperature = 25.1 °C; average monthly rainfall = 7.1 mm). We contrasted the physiological parameters of mature subordinate females caught during a trapping session towards the end of a prolonged dry period (1st to 15th of October 2004; Fig. 1) with those of mature subordinate females caught during a trapping session at the peak of the subsequent wet period (20th March to 17th of April 2005; Fig. 1).

Colonies were trapped by digging a short trench across a line of mole-hills to locate the underlying tunnel (typically at a depth of 20 to 80 cm) and then setting pipe traps baited with sweet potato in the line of the tunnel. Traps were typically checked every 1–3 h and any trapped animals immediately transferred to spacious individual urine collection traps (see below) and weighed using an electronic balance (Ohaus CS2000). Once a urine sample had been passed (or if nothing had been passed for >4 h), the animals were transferred to a large sand-lined box for housing with the other members of their colony and were sustained on sweet potato. Once the colony had been completely trapped out (gauged by an absence of activity at the trap site for 36 h) and urine and blood sampling had been completed, any unmarked animals (distinguished until now by their sex, weight and coat patterns) were marked with subcutaneous transponder chips and the entire colony was returned together to their original tunnel system.

A colony was defined as the group of one or more individuals caught from the same contiguous burrow system. Typically all colony

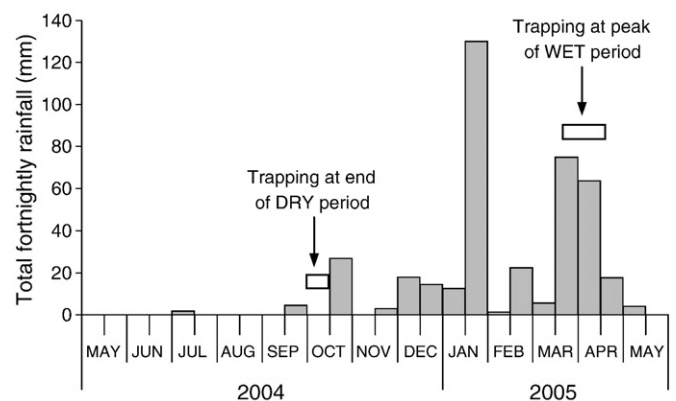


Fig. 1. Fortnightly rainfall patterns for the study period, indicating the two key trapping periods: one at to the end of the dry period and one at the peak of the wet period.

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